SYSTEMATICS OF THE *STEINDACHNERINA HYPOSTOMA* COMPLEX (PISCES, OSTARIPHYSI, CURIMATIDAE), WITH THE DESCRIPTION OF THREE NEW SPECIES

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Abstract. – The Steindachnerina hyposoma complex is revised and four species are recognized: S. hypostoma (Boulenger) widely distributed through the Rio Amazonas system upstream of Manaus; S. planiventris, new species, from the Rio Negro and Rio Madeira basins, and various localities along the Rio Amazonas upstream of Manaus; S. gracilis, new species, apparently endemic to the Rio Tocantins system of eastern Brazil; and S. quasimodoi, new species, of the western portions of the Amazon basin in Brazil and Peru. The four species have in common derived expansions of the mesethmoid and frontals that result in a reduction in the size of the cranial fontanel, and unite them as a monophyletic assemblage. A key to the species of the complex is provided.

Resumo. – O complexo Steindachnerina hypostoma é revisto e quatro espécies reconhecidas: S. hypostoma (Boulenger) amplamente distribuída no sistema do Rio Amazonas, acima de Manaus; S. planiventris, espécie nova, das bacias do Rio Negro e do Rio Madeira e várias localidades ao longo do Rio Solimões acima de Manaus; S. gracilis, espécie nova, aparentemente endêmica da bacia do Rio Tocantins no leste do Brasil; e S. quasimodoi, espécie nova, da parte oeste da Bacia Amazônica, no Brasil e Peru. As quatro espécies têm em commum expansões derivadas do mesetmóide e frontais que causam a redução em tamanho da fontanela craniana e unem estas quatro espécies em um grupo monofilético. Uma chave para as espécies do grupo é apresentada.

Boulenger (1887:172) described Curimatus hypostoma on the basis of four specimens collected by "Mr. W. Davis" in the "Ucayali River" of Peru. At the end of his brief description, he noted the very shallow body depth characteristic of the species. That feature is indeed striking when one compares this species to other curimatids, most of which have moderately to very deep bodies (see figures in Vari, 1982, 1984, in press a, b, c). Although this unusually shaped species was subsequently referred to by Eigenmann & Eigenmann (1891), Eigenmann (1910), Fowler (1942, 1950, 1975), and Fernández-Yépez (1948), among others, those citations were based on the original description without examination of other specimens. The only subsequent locality record of *Curimatus hypostoma* based on additional material was that of Eigenmann and Allen (1942:296) who reported on a series of specimens from various localities in the Amazon basin in Peru. Most recently Vari (1989) assigned *Curimatus hypostoma* to the speciose genus *Steindachnerina* Fowler. The limited number of references in the literature to *Steindachnerina hypostoma* are rather surprising given that the species is relatively common in many of the major river systems of the Amazon basin, and has a geographic distribution much wider than reported in the literature.

Collecting efforts in recent years throughout the Amazon basin have yielded large series of specimens typically identified as *Curimatus hypostoma*. The examination of these collections undertaken as part of more encompassing studies within the Curimatidae has revealed that this material actually encompasses four distinct, albeit similar, species that form a monophyletic subunit of the Curimatidae. The known distribution of the species of the clade encompasses both the main Rio Amazonas basin and the associated Rio Tocantins system of eastern Brazil. The shared derived features of these species are discussed, and a key to, and descriptions of the species are provided.

Materials and methods. - Counts and measurements were taken using the methods outlined in Vari (1982, 1984, in press a, b, c). In the case of new species the presented ranges of counts and measurements include values of all type specimens. The ranges of these values for Steindachnerina hypostoma include all specimens cited for which standard lengths (SL) are given. Values in square brackets in species descriptions are those of the holotype or lectotype. Information on localities and specimens examined in detail is arranged as in Vari (1982, 1984, in press a, b, c). Measurements are presented as proportions of standard length (SL) or head length (HL).

The following abbreviations for institutions are used: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Stanford University, now deposited at CAS (CAS-SU); Jacques Géry, personal collection (GC); Indiana University, collections now at various repositories (IU); Los Angeles County Museum of Natural History (LACM); Museum of Comparative Zoology, Cambridge (MCZ); Museu de Zoologia da Universidade de São Paulo (MZUSP); Naturhistoriska Riksmuseet, Stockholm (NRM); Naturhistorisches Museum, Vienna (NMW); Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MHN-USM); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Steindachnerina hypostoma complex

Vari (1989) redefined Steindachnerina Fowler (1906) to include 32 nominal species or subspecies. Vari and Castro (1988) subsequently noted that Prochilodus stigmaturus Fowler is also a curimatid of the genus Steindachnerina rather than a prochilodontid. Steindachnerina has a wide distribution in lowland tropical South America on both sides of the Andean Cordilleras, but is by far most speciose in the Amazon basin, the region to which the Steindachnerina hypostoma complex is endemic. The members of Steindachnerina share a series of synapomorphous features of the first and second infraphyarnygobranchials, the mode of attachment of the ligament joining the second and third hypobranchials, and the form of the basihyal and its associated tooth-plate (see Vari [1989] synapomorphies 97 to 100). The four species of the Steindachnerina hypostoma complex are, in turn, characterized by derived modifications of the mesethmoid and frontals of lesser universality that are reflected in the relative size and form of the cranial fontanel.

Species of Steindachnerina outside of the hypostoma complex and curimatids in general have relatively extensive dorsomedian cranial fontanels extending from the supraoccipital to the mesethmoid (e.g., S. bimaculata, Fig. 1A). In those outgroup taxa the anterior two-thirds of the relatively large opening is delimited laterally by widely separated frontals. The medial margins of the frontals anterior to the epiphyseal bar are nearly parallel or converge very gradually anteriorly. Anteriorly the fontanel is bordered by a distinct notch situated in the middle of the posterior border of the mesethmoid. This arrangement of bones along an extensive fontanel is hypothesized as primitive within Steindachnerina given its



Fig. 1. Dorsal view of anterior portion of cranial fontanel and proximate bones of A) *Steindachnerina bimaculata*, USNM 261450, 76.4 mm SL; B) *Steindachnerina quasimodoi*, USNM 293042, 76.0 mm SL; C) *Steindachnerina planiventris*, USNM 267987, 62.1 mm SL; D) *Steindachnerina gracilis*, USNM 293034, 63.4 mm SL; and E) *Steindachnerina hypostoma*, CAS 63192 (formerly IU 15825), 82.00 mm SL. Abbreviations: EB—epiphyseal bar; FR—frontal; ME—mesethmoid; P—Parietals. Mesethmoid and parietals truncated, horizontal lines indicate cranial fontanel.

general distribution in that genus and other curimatids.

The species of the S. hypostoma complex demonstrate marked changes in the morphology of those portions of the mesethmoid and frontals bordering the cranial fontanel. All four species lack the extension of the fontanel into the posterior portion of the mesethmoid. The posteromedial region of the mesethmoid is instead developed posteriorly into a triangular process (Fig. 1B to E). More striking is the expansion in all four species of the anteromedial portions of the frontals and the associated pronounced reduction of the portion of the cranial fontanel anterior of the epiphyseal bar. As a consequence of this expansion the anteromedial margins of the frontals no longer extend roughly in parallel. The margins of the bones instead converge and are either separated by a small gap (Steindachnerina quasimodoi, Fig. 1B), or are in contact medially to varying degrees (S. planiventris, S. gracilis, S. hypostoma, Fig. 1C-E).

Both the extension of the posteromedial portion of the mesethmoid and the medial expansion of the frontals in the four species of the *Steindachnerina hypostoma* complex are derived relative to the conditions of these bones in outgroups. These synapomorphies support a hypothesis that *S. hypostoma*, *S. gracilis*, *S. quasimodoi*, and *S. planiventris* are a monophyletic lineage within *Steindachnerina*.

Key to the species of the *Steindachnerina hypostoma* complex

- 2. Lateral-line scales to hypural joint 50 to 54 S. gracilis, new species
- 3. Greatest body depth in specimens over 50 mm SL 0.30–0.34 of SL, body with distinctly humped dorsal profile (Figs. 6, 7); frontals separated by slight gap anteriorly (Fig. 1B)

Steindachnerina hypostoma (Boulenger, 1887) Figs. 1–4, Table 1

Curimatus hypostoma Boulenger, 1887:172 [type locality: Ucayali River]. – Vari, 1989:tabs. 2, 3 [phylogenetic relationships].



Fig. 2. Steindachnerina hypostoma, USNM 229190, 93.2 mm SL; Brazil, Amazonas, Rio Solimões, Ilha Machantaria.

- Curimatus hypostomus, Eigenmann & Eigenmann, 1889:426 [reference]. Eigenmann & Eigenmann, 1891:47 [reference]. Eigenmann, 1910:422 [reference].
 Curimata hypostoma, Fowler, 1942:208 [reference]. Fowler, 1945:116 [reference]. Eigenmann & Allen, 1942:296 [Peru: Río Huallaga, Yurimaguas; Río Morona; Río Paranapura, Yurimaguas (in part)]. Fowler, 1945:116 [reference]. Géry, 1977:235 [reference]. Ortega & Vari, 1986:11 [Peru, Amazon basin; common name].
- Curimata hypostoma hypostoma, Fowler, 1950:285 [literature compilation].
- Steindachnerina hypostomus, Fernández-Yépez, 1948:58 [assignment to Steindachnerina].
- Steindachnerina hypostoma, Fowler, 1975: 375 [reference].

Diagnosis. — The absence of a discrete patch of dark pigmentation at the base of the middle rays of the dorsal fin distinguishes S. hypostoma from the other members of the complex, all of which have such pigmentation developed to some degree. The 46 to 50 lateral line scales of S. hypostoma further differentiate the species from S. gracilis which has 50 to 54 scales in that series and from S. quasimodoi and S. planiventris which have 40 to 46. Differences in other meristic and morphometric features also discriminate S. hypostoma from the remaining members of the complex (Table 1).

Description.—Body elongate, relatively wide, particularly in ripe females. Dorsal profile of head straight or very slightly convex. Dorsal profile of body smoothly curved, slightly convex from rear of head to origin of dorsal fin; straighter and slightly postero-



Fig. 3. Steindachnerina hypostoma, USNM 278579, 48.9 mm SL; Bolivia, Pando, Río Madre de Dios, Laguna San Luis.



Fig. 4. Map of northern South America showing geographic distribution of *Steindachnerina hypostoma* (dots) and *Steindachnerina gracilis* (stars). Type localities: 1, Rio Aripuana, Aruanã; 2, Rio Tocantins, Tucuruí; and 3, Río Ucayali (exact collection site of syntypes of *Curimatus hypostoma* unknown). Some symbols represent more than one lot and/or collecting locality.

ventrally slanted at base of dorsal fin, straight or very gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel more pronounced proximate to fin; body surface smoothly rounded transversely posterior to fin. Ventral profile of body very gently curved from tip of lower jaw to caudal peduncle. Prepelvic region wide, distinctly flattened, with five series of scales in transverse series across flattened surface. Pelvic fins distinctly separated medially. Post-pelvic region somewhat flattened proximate to pelvic fin, gradually becoming transversely rounded posteriorly.

Greatest body depth at origin of dorsal fin, depth 0.24–0.27 [0.25]; snout tip to origin of dorsal fin 0.44–0.48 [0.45]; snout tip to origin of anal fin 0.80–0.85 [0.82]; snout tip to insertion of pelvic fin 0.48–0.53 [0.48]; snout tip to anus 0.70–0.75 [0.72]; origin of dorsal fin to hypural joint 0.56–0.60 [0.59]. Dorsal-fin margin pointed; anteriormost rays 2.8–3.5 times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.17–0.20 [0.18], extends slightly over three-quarters of distance to vertical through insertion of pelvic fin. Pelvic-fin margin obtusely pointed, length of pelvic fin 0.19–0.22 [0.20], reaches about threefifths of distance to origin of anal fin. Caudal fin distinctly forked. Adipose dorsal fin well developed. Anal fin emarginate, anteriormost branched rays approximately two and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.12 [0.11].

Head distinctly pointed in profile, more so in larger specimens, head length 0.24– 0.28 [0.27]; upper jaw distinctly longer than lower, mouth inferior; snout length 0.28– 0.31 [0.28]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.28–0.34 [0.29]; adipose eyelid present, poorly developed, with rotund opening over center of eye; length of postorbital portion of head 0.39– 0.45 [0.43]; gape width 0.28–0.34; interorbital width 0.38–0.42 [0.39].

Pored lateral line scales from supracleithrum to hypural joint 46 to 50 [49]; all scales of lateral line pored, canals in scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal fin base; $8\frac{1}{2}$ to $9\frac{1}{2}$ [$8\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $6\frac{1}{2}$ to $7\frac{1}{2}$ [7] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (iii,9 rare, when three unbranched rays present, first very short) [ii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 14 to 16 [14]; pelvic-fin rays i,8 [i,8].

Total vertebrae 35 (8), 36 (86), 37 (2).

Color in alcohol.—Overall coloration of specimens retaining guanine on scales silvery to silvery-golden, darker on dorsal portions of head and body. Specimens fixed in formalin and lacking guanine on scales with overall ground coloration tan to light brown, darker on dorsal portions of head and body (Fig. 2). Pores of lateral line scales outlined by dark pigmentation in some specimens.

	hypostoma	gracilis	quasimodoi	planiventris
	Morph	ometrics		
1. Greatest body depth	0.24-0.27	0.25-0.27	0.27-0.34*	0.27-0.30
2. Snout to pelvic-fin origin	0.48-0.53	0.53-0.55	0.50-0.54	0.52-0.56
3. Snout to anus	0.70-0.75	0.73-0.75	0.75-0.76	0.72-0.76
4. Pelvic-fin length	0.19-0.22	0.19-0.21	0.23-0.26	0.19-0.23
5. Snout length	0.28-0.31	0.31-0.34	0.31-0.34	0.33-0.36
6. Orbital diameter	0.28-0.34	0.32-0.35	0.31-0.37	0.29-0.33
7. Postorbital length	0.39-0.45	0.39-0.42	0.36-0.40	0.36-0.41
	Me	ristics		
Lateral line scales	45-50	50-54	40-46	40-46
Scale rows between dorsal-fin				
origin and lateral line	81/2-9	10-101/2	71/2-9	61/2-8
Scale rows between anal-fin				
origin and lateral line	61/2-71/2	61/2-71/2	51/2-61/2	51/2-61/2

Table 1.—Range of morphometrics and meristic features of species useful in discriminating species of *Stein-dachnerina hypostoma* complex. Measurements 1 to 4 are proportions of standard length; 5 to 7 are proportions of head length.

* 0.30-0.34 in specimens of 50 mm SL or greater.

Lateral line pigmentation more intense, when present, in smaller individuals, sometimes forming distinct mid-lateral stripe (Fig. 3). Deeper lying dusky mid-lateral band extends from supracleithrum to caudal peduncle; typically more obvious in smaller individuals; masked in specimens retaining guanine on scales. Caudal-fin rays outlined by series of small chromatophores, lower lobe of caudal fin dusky. Anterior margin of dorsal fin sometimes dusky, but without spot of dark pigmentation at base of middle rays; other fins hyaline.

Distribution. – Amazon basin upstream of Manaus, Brazil (Fig. 4).

Common name. – Chio-chio (Ortega & Vari, 1986:11, Peru).

Remarks.—Boulenger (1887a) described *Curimatus hypostoma* on the basis of four specimens from an unspecified location along the Rio Ucayali of Peru. An 87.5 mm SL syntype (BMNH 1881.5.13:105), which is in the best overall condition, is designated as the lectotype. The remaining specimens in the type series (BMNH 1881.5.13:106– 108) thus become paralectotypes.

Allen (in Eigenmann & Allen 1942:297) described a nominal subspecies *Curimata*

hypostoma hastata on the basis of a single specimen from Puerto Bermudez, on the Río Pichis, Peru. A re-examination of the holotype (CAS 19881, formerly IU 17859) reveals that although it is a member of the Steindachnerina clade, it is not conspecific with S. hypostoma, and indeed is not even a member of the S. hypostoma complex, but rather a specimen of S. dobula (Günther). The specimens identified by Eigenmann & Allen (1942:296) as Curimatus hypostoma are an admixture of S. hypostoma and S. dobula (e.g., IU 17858 from Yurimaguas, Río Paranapura). The complexity of that series of specimens may account, at least in part, for Allen's assignment of hastata as a subspecies of hypostoma.

Material examined. – 286 specimens (70, 55.1–98.3).

PERU: Ucayali River, BMNH 1881.5.13: 105, 1 (87.5, lectotype of *Curimatus hypostoma*); BMNH 1881.5.13:106–108, 3 (85.5–90.0, paralectotypes of *Curimatus hypostoma*). *Loreto*; Shansho Caño, USNM 175867, 1. Beirut, near mouth of Río Ambiyacu, USNM 261452, 2 (76.3–77.8). Rio Javari, near Petropolis, USNM 261438, 1 (78.3). Río Amazonas, Ramon Castilla,

USNM 261512, 1 (79.6). Río Javari system, Río Galvez near mouth, NRM SOK/ 1984314.4058, 3. Río Huallaga, Yurimaguas, USNM 293094, 1 (98.3); CAS 63191, 2 (84.0-86.8, formerly IU 17858); USNM 167802, 5 (83.0-91.3); CAS 63192, 3 (83.8-92.0; formerly IU 15825). Yurimaguas, Río Paranapura, IU 17858, 2 (part of lot). Huanuco; Río Pachitea, Tournavista, USNM 293092, 1. Ucayali; Río Ucayali, Pucallpa, USNM 261513, 5 (80.1-91.2); USNM 261489, 5 (65.8-96.5); USNM 261465, 6 (3, 55.3-59.8); USNM 261477, 5 (3, 70.4-83.4); AMNH 35686, 1 (70.0); USNM 261493, 6; USNM 261496, 2; USNM 261488, 6; USNM 293087, 1. Río Neshuyo where crossed by Pucallpa-Huanuco Road, USNM 261401, 1. Río Ucayali, Masisea, USNM 243237, 3 (60.4-63.4); USNM 293090, 5; USNM 293095, 10. Río Ucayali, Nuevo San Juan near Masisea, USNM 293089, 3. Río Ucayali, Utuquinia, USNM 293091, 1. BRAZIL: Amazonas; Ilha da Machantaria, USNM 293096, 1 (89.0); GC, 3 (86.3-92.0); USNM 229190, 1 (94.1); USNM 229187, 1; USNM 229185, 2. Lago Janauacá and vicinity, MZUSP 21699, 2. Rio Solimões, Fonte Boa, MZUSP 20947, 6 (77.5-92.8); MZUSP 20957, 2 (81.5-84.9). Rio Juruá, BMNH 1897.12.1: 88-100, 8 (4, 55.1-60.7). Ilha Xibeco, Rio Solimões above mouth of Rio Jutai, MZUSP 21018, 1 (91.4); MZUSP 21017, 6 (3, 79.3-83.7). Rio Solimões, Ilha Sorubim above Coari, MZUSP 20926, 161 (6, 68.5-84.5). Rio Solimões, Tefé, mouth of Rio Japurá, MZUSP 27360, 1. Rio Solimões, Benjamin Constant, Costa do Capacete, MZUSP 27379, 1. Santo Antonio do Iça, mouth of Rio Iça, MZUSP 21000, 4 (75.0-82.8).

Steindachnerina gracilis, new species Figs. 1, 4-5, Table 1

Diagnosis.—The 50 to 54 scales in the lateral line to the hypural joint and 10 or $10\frac{1}{2}$ scales above the lateral line to the origin of the dorsal fin distinguish *S. gracilis*

from S. planiventris and S. quasimodoi which have 40 to 46 lateral line scales and $7\frac{1}{2}$ to $8\frac{1}{2}$ and $7\frac{1}{2}$ to $9\frac{1}{2}$ scales above the lateral line respectively, and from S. hypostoma which has 46 to 50 lateral line scales and $8\frac{1}{2}$ to $9\frac{1}{2}$ scales above the lateral line. Steindachnerina gracilis, which has a spot of dark pigmentation at the base of the middle rays of the dorsal fin is readily separable from S. hypostoma which lacks such pigmentation. A variety of meristic and morphometric features also distinguish S. gracilis from the three other species within the complex (Table 1).

Description. - Body elongate, moderately wide transversely. Dorsal profile of head straight or very slightly concave. Dorsal profile of body straight or very slightly convex from rear of head to origin of dorsal fin; straight and very slightly posteroventrally slanted at base of dorsal fin, straight or gently convex from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body with distinct median keel anterior to dorsal fin, keel more pronounced proximate to dorsal fin; body surface smoothly rounded transversely posterior to fin. Ventral profile of body very slightly convex from tip of lower jaw to caudal peduncle. Pre-pelvic region wide, distinctly flattened transversely, with obtuse lateral angles in body wall, five series of scales transversely across flattened region. Pelvic fins distinctly separated medially. Post-pelvic region somewhat flattened proximate to pelvic fin, gradually becoming transversely rounded posteriorly.

Greatest body depth at origin of dorsal fin, depth 0.25–0.27 [0.26]; snout tip to origin of dorsal fin 0.46–0.49 [0.46]; snout tip to origin of anal fin 0.84–0.86 [0.83]; snout tip to insertion of pelvic fin 0.53–0.55 [0.53]; snout tip to anus 0.73–0.75 [0.73]; origin of dorsal fin to hypural joint 0.54–0.58 [0.56]. Dorsal-fin margin obtusely pointed, anteriormost rays slightly less than three times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.17–0.21 [0.19], extends about three-quarters dis-



Fig. 5. Steindachnerina gracilis, new species, holotype, MZUSP 4857, 63.5 mm SL; Brazil, Goiás, Rio Araguaia, Aruanã.

tance to vertical line through insertion of pelvic fin. Pelvic-fin margin obtusely pointed, length of pelvic fin 0.19–0.21 [0.20], reaches about three-fifths distance to origin of anal fin. Caudal fin distinctly forked. Adipose dorsal fin well developed. Border of anal fin emarginate, anteriormost branched rays about two and one-half times length of ultimate ray. Caudal peduncle depth 0.11– 0.12 [0.11].

Head distinctly pointed in profile, head length 0.27–0.29 [0.27]; upper jaw distinctly longer than lower, mouth inferior; snout length 0.31–0.34 [0.32]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.32–0.35 [0.32]; adipose eyelid poorly developed, with rotund opening over center of eye; length of postorbital portion of head 0.39–0.42 [0.39]; gape width 0.32–0.35 [0.33]; interorbital width 0.39–0.42 [0.41].

Pored lateral line scales from supracleithrum to hypural joint 50 to 54 [53]; all scales of lateral line pored, canals in scales straight; 3 to 5 series of scales extend beyond hypural joint onto caudal fin base; 10 to $10\frac{1}{2}$ [$10\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $6\frac{1}{2}$ to $7\frac{1}{2}$ [$7\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [ii,7]; pectoral-fin rays 15 to 17 [16]; pelvicfin rays i,8 [i,8]. Total vertebrae 35 (8), 36 (5).

Color in alcohol. - Overall coloration of specimens retaining guanine on scales silvery golden, darker on dorsal portions of head and body. Overall coloration of specimens fixed in formalin and lacking guanine on scales tan to light brown, darker on dorsal portions of head and body. Pores of lateral line scales outlined by dark pigmentation, spots forming irregular mid-lateral stripe. Deeper lying dusky stripe extending from supracleithrum to caudal peduncle, stripe masked in individuals retaining guanine on scales. Anterior margin and distal portions of dorsal fin dusky. Distinct dusky spot on middle rays of dorsal fin slightly above their insertion, spot faint in some individuals. Rays of caudal fin outlined by series of small chromatophores; lower lobe of caudal fin dusky. Other fins hyaline.

Distribution.—Rio Tocantins system (Fig. 4).

Etymology.—The name *gracilis,* from the Latin for slender, refers to the relatively elongate body of the species.

Type material.—16 specimens, 56.7–73.4 mm SL.

Holotype. – BRAZIL. Goiás. Rio Araguaia, Aruanã (approx. 14°54'S, 51°05'W), 63.5 mm SL; Excursion de Departamento de Zoologia (now MZUSP), MZUSP 4847, 15 to 19 Sep 1966.

Paratypes.—BRAZIL: *Goiás*; Rio Araguaia, Aruanã, MZUSP 38591, 2 (56.7–63.5; taken with holotype); USNM 293035, 1 (67.2; taken with holotype); USNM 191632, 1 (approx. 73.4), H. A. Axelrod, 1960. *Pará*:



Fig. 6. *Steindachnerina quasimodoi*, new species, holotype, USNM 293041, 88.9 mm SL; Peru, Loreto, Río Yavari, near Petropolis.

Rio Tocantins, lagoons along margin of river near Tucuruí (approx. 3°42'S, 49°27'W), MZUSP 38592, 6 (61.5–64.9); USNM 293034, 6 (57.4–65.4, 2 specimens cleared and counterstained for cartilage and bone), Expediçao Permanente da Amazônas, 14 Sep 1970.

Steindachnerina quasimodoi, new species Figs. 1, 6-10, Table 1

Diagnosis. — The 40 to 46 lateral line scales to the hypural joint distinguish S. quasimodoi from S. gracilis which has 50 to 54 scales in that series and S. hypostoma which has 46 to 50. The presence of a discrete spot of dark pigmentation in the basal portions of the middle rays of the dorsal fin further separates S. quasimodoi from S. hypostoma which lacks that pigmentation. Other differences in meristic and morphometric features further differentiate S. quasimodoi from *S. hypostoma* and *S. gracilis* (Table 1). Specimens of *S. quasimodoi* of greater than 50 mm SL are distinguished from comparably sized individuals of *S. planiventris* in their greatest body depths (0.30–0.34 of SL versus 0.27–0.30, Fig. 8), by differences in the degree of convexity of the dorsal surface of the body (Figs. 6, 7, 11), length of the pelvic fins (0.23–0.26 of SL versus 0.19–0.23, Fig. 9), and degree of contact of frontals anterior to cranial fontanel (Fig. 1B, C). The relative orbital width and length of the postorbital region of the head also discriminate the species to a degree (Table 1).

Description. – Body elongate, deeper bodied in larger specimens, somewhat compressed laterally. Dorsal profile of head slightly convex anterior to vertical through nostrils, striaght from that line to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin, slope more pronounced with increasing size;



Fig. 7. Steindachnerina quasimodoi, new species, paratype, USNM 283040, 53.7 mm SL; Brazil, Rio Javari, opposite Colonia Angamos, Peru.



Fig. 8. Plot of greatest body depth (GBD) against standard length (SL), both in millimeters, and regression lines for *Steindachnerina quasimodoi* (dots, Y = -4.052 + 0.380X) and *Steindachnerina planiventris* (stars, Y - 4.089 + 0.351X) (some symbols represent more than one data point).

straight and slightly posteroventrally slanted at base of dorsal fin in juveniles, adults with angle more pronounced; straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to



Fig. 9. Plot of length of pelvic fin (PFL) against standard length (SL), both in millimeters and regression lines, for *Steindachnerina planiventris* (dots, Y = 0.851 + 0.185X) and *Steindachnerina quasimodoi* (stars, Y = 0.561 + 0.241X), (some symbols represent more than one data point).



Fig. 10. Map of northern South America showing geographic distribution of *Steindachnerina quasimodoi* (stars) and *Steindachnerina planiventris* (dots). Type localities: 1, Rio Machado; and 2, Río Yavari, Petropolis. Some symbols represent more than one lot and/ or collecting locality.

fin. Ventral profile of body very gently curved from tip of lower jaw to origin of anal fin, sigmoid from that point to caudal peduncle. Pre-pelvic region broadly flattened, with three irregular series of scales across flattened ventral surface. Scale series of pre-pelvic region flanked on each side by series of scales bent to conform to shape of lateral angles of body. Obtuse median keel posterior to pelvic fin insertion. Secondary obtuse keel on each side of post-pelvic portion of body two scales dorsal of ventral midline.

Greatest body depth at origin of dorsal fin, depth 0.27-0.34 (0.30-0.34 in specimens above 50 mm SL) [0.33]; snout tip to origin of dorsal fin 0.47-0.50 [0.49]; snout tip to origin of anal fin 0.84-0.86 [0.86]; snout tip to insertion of pelvic fin 0.50-0.54 [0.50]; snout tip to anus 0.75–0.78 [0.76]; origin of dorsal fin to hypural joint 0.54-0.59 [0.59]. Dorsal-fin margin poionted, less so with increasing age; anteriormost rays about three to three and one-half times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.19-0.21 [0.21], extends posteriorly to point about two scales anterior of vertical through insertion of pelvic fin. Pelvic-fin margin

pointed, length of pelvic fin 0.23–0.26 [0.26], reaches two-thirds distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Anal fin emarginate, anteriormost branched rays about three to three and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.13 [0.13].

Head distinctly pointed, head length 0.27– 0.33 [0.28]; upper jaw much longer than lower, mouth inferior; snout length 0.31– 0.34 [0.33]; nostrils very close, anterior circular, posterior crescent shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.31–0.37 [0.32]; adipose eyelid present, more developed in larger specimens, particularly anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.36–0.40 [0.36]; gape width 0.30– 0.35 [0.33]; interorbital width 0.36–0.43 [0.42].

Pored lateral line scales from supracleithrum to hypural joint 40 to 46 [44]; all scales of lateral line pored, canals in scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal fin base; $7\frac{1}{2}$ to $9\frac{1}{2}$ [$8\frac{1}{2}$] scales in transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to $6\frac{1}{2}$ [$6\frac{1}{2}$] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 15 to 17 [16]; pelvicfin rays i,8 or rarely i,7,i [i,8].

Total vertebrae 35 (11), 36 (20).

Color in life.—(The following description is based on a color transparency of a specimen captured in the Rio Javari by S. O. Kullander). Overall coloration bright silver, somewhat darker on dorsal portions of head and body. Iris silver. Fins yellowish with light margins. Dorsal fin with a small dark patch on basal portion of middle rays.

Color in alcohol.—Ground coloration of specimens lacking guanine on scales tan, darker on dorsal portion of body. Dorsal portion of head dusky. Margins of scales on

lateral and dorsal portions of body outlined by series of small chromatophores in juveniles. Pigmentation field expanded in larger specimens to cover exposed surface of scales, particularly dorsally. Mid-dorsal line somewhat darker, particularly immediately anterior of dorsal fin. Pores in lateral line scales outlined dorsally and ventrally by chromatophores. Dorsal fin with diffuse patch of dark pigmentation on basal portion of membranes between third and fifth ray. Dorsal and caudal fins dusky. Adipose dorsal fin margin dusky. Anal fin hyaline or with scattered chromatophores. Paired fins hyaline.

Distribution.—Río Javari (=Rio Yavari) system of Peru and Brazil, and proximate portions of Peruvian Amazon (Fig. 10).

Etymology.—The specific name *quasi-modoi* is taken from Quasimodo, the misunderstood hunchback bell-ringer of the Cathedral in Victor Hugo's novel *Notre Dame de Paris*, and refers to the pronounced humped dorsal profile of the body in larger specimens of the species.

Type material. – 39 specimens, 34.3–122.6 mm SL.

Holotype.-PERU. Loreto. Río Javari, near Petropolis; Hérnan Ortega, 2 Oct 1982, USNM 293041, 1 (88.9).

Paratypes.-PERU. Loreto. 13 specimens taken with holotype, USNM 293042, 7 (49.7-122.6, two specimens cleared and counterstained for cartilage and bone); MHN-USM 1698, 4 (50.7-100.6); MZUSP 38593, 2 (58.4-59.6).

BRAZIL: *Amazonas*; Rio Javari system, immediately downstream of confluence of Rio Jaquirana and Rio Gálvez; S. Kullander, et al., 31 July 1984. NRM SOK/ 1984312.4093, 9 (33.3–121.8); MZUSP 38594, 3 (50.1–53.6). Rio Javari system, opposite Colonia Angamos, Peru; S. Kullander, et al., 5 Aug 1984, NRM SOK/ 1984317.4091, 7 (40.0–69.2); MHN-USM 1699, 3 (49.8–57.0); USNM 293040, 3 (34.3–61.5).

The following non-type specimens were also examined:



Fig. 11. Steindachnerina planiventris, new species, holotype, MZUSP 35857, 65.7 mm SL; Brazil, Rondonia, Rio Machado, near mouth.

PERU: *Loreto*; Río Ampiyacu, near the mouth, USNM 175868, 1 (48.4). Pebas, CAS-SU 36888, 1 (81.7).

Steindachnerina planiventris, new species Figs. 1, 8-11, Table 1

Curimatus bimaculatus, Eigenmann and Eigenmann, 1889:422 [in part, specimens from Iça, Brazil].

Diagnosis. - The 40 to 46 lateral in scales to the hypural joint distinguish S. planiventris from S. gracilis which has 50 to 54 scales in that series and S. hypostoma which has 46 to 50. The presence of a discrete spot of dark pigmentation in the basal portions of the middle rays of the dorsal fin further separates S. planiventris from S. hypostoma which lacks that pigmentation. Other differences in meristic and morphometric features further differentiate S. planiventris from S. hypostoma and S. gracilis (Table 1). Specimens of S. planiventris of greater than 50 mm SL are distinguished from comparably sized individuals of S. quasimodoi in their greatest body depths (0.27-0.30 of SL versus 0.30-0.34, Fig. 8), differences in the degree of convexity of the dorsal surface of the body (Figs. 7, 11), pelvic-fin length (0.19-0.23 of SL versus 0.23-0.26, Fig. 9), and degree of contact of the frontals anterior of the cranial fontanel (Fig. 1C, B). The relative orbital width and length of the postorbital region of the head also discriminate the species to a degree (Table 1).

Description.-Body elongate, slightly compressed. Dorsal profile of head distinctly

convex anterior to vertical through nostrils, slightly convex or straight from that point to rear of head. Dorsal profile of body slightly convex from rear of head to origin of dorsal fin; straight and slightly posteroventrally slanted at base of dorsal fin, straight from base of last dorsal-fin ray to caudal peduncle. Dorsal surface of body transversely rounded anteriorly, with indistinct median keel immediately anterior to dorsal fin, smoothly rounded transversely posterior to fin. Ventral profile of body gently curved from tip of lower jaw to caudal peduncle. Pre-pelvic region distinctly flattened, with three longitudinal series of scales on ventral flattened surface. Ventral scale series flanked on each side by series of scales bent to conform to shape of lateral angles of body. Barely discernable median keel posterior to pelvic-fin insertion. Secondary obtuse keel on each side of postventral portion of body about two scales dorsal of ventral midline.

Greatest body depth at origin of dorsal fin, depth 0.27–0.30 [0.29]; snout tip to origin of dorsal fin 0.46–0.50 [0.49]; snout tip to origin of anal fin 0.83–0.87 [0.87]; snout tip to insertion of pelvic fin 0.52–0.56 [0.54]; snout tip to anus 0.72–0.76 [0.75]; origin of dorsal fin to hypural joint 0.54–0.59 [0.57]. Dorsal-fin margin pointed, less so with increasing age; anteriormost rays three to three and one-half times length of ultimate ray. Pectoral-fin margin pointed; length of pectoral fin 0.18–0.23 [0.20], extends about three-quarters distance to vertical through insertion of pelvic fin. Pelvic-fin margin pointed, length of pelvic fin 0.19–0.23 [0.21], reaches about two-thirds distance to origin of anal fin. Caudal fin forked. Adipose dorsal fin well developed. Anal fin barely emarginate, anteriormost branched rays three to three and one-half times length of ultimate ray. Caudal peduncle depth 0.11–0.12 [0.12].

Head distinctly pointed, head length 0.26– 0.31 [0.30]; upper jaw distinctly longer than lower, mouth inferior; snout length 0.33– 0.36 [0.33]; nostrils very close, anterior circular, posterior crescent-shaped with aperture closed by thin flap of skin separating nares; orbital diameter 0.29–0.33 [0.30]; adipose eyelid present, moderately developed, more so anteriorly, with broad vertically ovoid opening over center of eye; length of postorbital portion of head 0.36– 0.41 [0.38]; gape width 0.28–0.34 [0.32]; interorbital width 0.38–0.44 [0.40].

Pored lateral line scales from supracleithrum to hypural joint 40 to 46 [41]; all scales of lateral line pored, canals in scales straight; 4 to 6 series of scales extend beyond hypural joint onto caudal fin base; $6\frac{1}{2}$ to $8\frac{1}{2}$ [7¹/₂] scales in transverse series from origin of dorsal fin to lateral line; $5\frac{1}{2}$ to $6\frac{1}{2}$ [5¹/₂] scales in transverse series from lateral line to origin of anal fin.

Dorsal-fin rays ii,9 or iii,9 (when three unbranched rays present, first very short) [iii,9]; anal-fin rays ii,7 or iii,7 (when three unbranched rays present, first very short) [iii,7]; pectoral-fin rays 15 to 17 [15]; pelvicfin rays i,8 [i,8].

Total vertebrae 34 (19), 35 (109), 36 (7).

Color in alcohol.—Specimens retaining guanine on scales with overall coloration golden, somewhat purplish dorsally. Ground pigmentation in specimens lacking guanine on scales tan to light brown, darker on dorsal portions of head and body. Scales on lateral and dorsal surfaces of body with margins outlined by series of small chromatophores; chromatophore series most developed dorsally, increasingly less so ventrally. Dorsal fin with patch of dark chromatophores on basal portion of membranes between third and fifth rays. Median fins, particularly lower lobe of caudal fin in some individuals, dusky. Paired fins hyaline.

Distribution.—Rio Madeira and Rio Negro basins, main channel and tributaries of middle Rio Solimões (Fig. 10).

Etymology.—The specific name, *plani*ventris, from the Latin planum, flat, and venter, belly, refers to the flattened ventral surface of the body in this species.

Remarks.—In their revision of the thenknown species of curimatids, Eigenmann and Eigenmann (1889:42) listed extensive series of specimens of *Curimatus bimaculatus* Steindachner (=*Steindachnerina bimaculata*) from various central and western Amazonian localities. At least some of the specimens from "Iça" (the Rio Iça of western Amazonas State in Brazil) are *Steindachnerina planiventris* (USNM 120250).

Type material.—80 specimens, 53.5–78.8 mm SL.

Holotype. – BRAZIL: Rondonia; Rio Machado, near mouth (approx. 8°03'S, 62°53'W); M. Goulding, 4 Sep 1980, MZUSP 38587, 1 (65.7).

Paratypes. – BRAZIL: Rondonia; 35 specimens taken with holotype: MZUSP 38588, 17 (55.5–74.1); USNM 267986, 18 (56.3–78.8). Rio Machado, Jauari, River Channel Beach; M. Goulding, 5 Sep 1980, USNM 267989, 18 (46.2–67.8), MZUSP 38590, 18 (53.5–65.2). Rio Machado, Santo Antonio; M. Goulding, 3 Sep 1980, USNM 267987, 6 (56.5–65.1, two specimens cleared and counterstained for cartilage and bone), MZUSP 38589, 5 (59.0–67.9).

The 157 following non-type specimens were also examined:

BRAZIL: Rio Juruá, BMNH 1897.12.1: 88–100, 13. *Rondonia*; Rio Machado, Cururu, USNM 267988, 8. *Roraima*: Rio Branco, Boa Vista, NMW 68887, 9; 1 NMW 68888, 10; NMW 68889, 4; NMW 68890, 8; NMW 68892, 5; NMW 68897, 1. Rio Branco, 20 km below Boiaçu, MZUSP 21164, 4 (49.3–53.7). Conceiçao (? =Conceiçao do Mau), NMW 68898, 6. Rio Branco, Serra Grande, 15 miles from Boa Vista, NMW 68885, 6 (53.1–87.0); NMW 68893, 3; NMW 68896, 2; NMW 697355, 4. *Amazonas*; Rio Negro, just below mouth of Rio Branco, USNM 293097, 22 (11, 52.5–80.6). Rio Negro, Anvilhanas, Municipio de Ayrão, USNM 293098, 7. Rio Solimões, Ilha Sorubim, above Coari, MZUSP uncat., 24 (62.3–71.3). Rio Solimões, Coari, USNM 293099, 12. Rio Solimões, near Ilha Baruruá, above mouth of Rio Jutaí, MZUSP 20987, 3 (2, 63.2–71.7). Rio Solimões, Ilha Xibeco, above mouth of Rio Jutaí, MZUSP uncat., 1 (73.8). Iça, USNM 120250, 5 (formerly MCZ 19571).

BOLIVIA: *Beni*; Río Mamoré, Puerto Siles, AMNH uncat., 2 (65.7–73.5).

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Literature Cited

- Boulenger, G. A. 1887. Description of South American characinoid fishes.—Annals and Magazine of Natural History 9:172–174.
- Eigenmann, C. H. 1910. Catalogue of the fresh-water fishes of tropical and south temperate America.—Report of the Princeton University Expedition to Patagonia, 1896–1899, 3 (Zoology, 4): 375–511.
- —, & W. R. Allen. 1942. Fishes of western South America. I. The intercordilleran and amazonian lowlands of Peru. II. The high pampas, Bolivia, and Northern Chile. With a revision of the peruvian Gymnotidae, and of the genus Orestias. 494 p. Lexington: University of Kentucky.
 - —, & R. S. Eigenmann. 1889. A revision of the edentulous genera of the Curimatinae.—Annals of the New York Academy of Sciences 4:409– 440.
- , & —, 8 1891. A catalogue of the freshwater fishes of South America.—Proceedings of the United States National Museum 14:1–81.
- Fernández-Yépez, A. 1948. Los curimatidos (peces fluviales de Sur America), catalogo descriptivo

con nuevas adiciones genericas y especificas.— Boletín Taxonómico del Laboratorio de Pesquería de Caiquire 1:1–86.

- Fowler, H. W. 1906. Further knowledge of some heterognathus fishes, Part I.—Proceedings of the Academy of Natural Sciences of Philadelphia, 58:293-351.
- ———. 1942. Los peces del Perú.—Boletin Museo de Historia Natural "Javier Prado." Lima 6: 206–222.
 - ——. 1945. Los peces del Perú.—Boletin Museo de Historia Natural "Javier Prado." Lima 7:1– 298.
 - —. 1950. Os peixes de áqua doce do Brasil (2a entrega).—Arquivos de Zoologia do Estado de São Paulo 6:205–404.
 - —. 1975. A catalogue of world fishes (XXIII). –
 Quarterly Journal of the Taiwan Museum 28(3):
 277–402.
- Géry, J. 1977. Characoids of the world. Neptune City, New Jersey, TFH Publications. 672 pp.
- Ortega, H., & R. P. Vari. 1986. Annotated checklist of the freshwater fishes of Peru.—Smithsonian Contributions to Zoology 437:1–25.
- Vari, R. P. 1982. Systematics of the neotropical characoid genus *Curimatopsis* (Pisces: Characoidei).—Smithsonian Contributions to Zoology 373: 1–28.
- ——. 1984. Systematics of the neotropical characiform genus *Potamorhina* (Pisces: Characiformes).—Smithsonian Contributions to Zoology 400:1–36.

- 1989. A phylogenetic study of the neotropical characiform family Curimatidae (Pisces: Ostariophysi).—Smithsonian Contributions to Zoology 471:1–71.
- in press a. Systematics of the neotropical characiform genus *Curimata* Bosc (Pisces: Characiformes).—Smithsonian Contributions to Zoology 474.
- in press c. Systematics of the neotropical characiform genus *Pseudocurimata* Fernández-Yépez (Pisces, Characiformes).—Smithsonian Contributions to Zoology 490.
- —, & R. M. C. Castro. 1988. Prochilodus stigmaturus Fowler, reassigned to the Curimatidae from the Prochilodontidae, with comments on other nominal curimatid and prochilodontid species treated by Fowler.—Copeia 1988(3):777– 780.

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